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A CYTOCHEMICAL FINE STRUCTURE STUDY OF PHAGOTROPHY IN A PLANKTONIC FORAMINIFER, *HASTIGERINA PELAGICA* (d'ORBIGNY)

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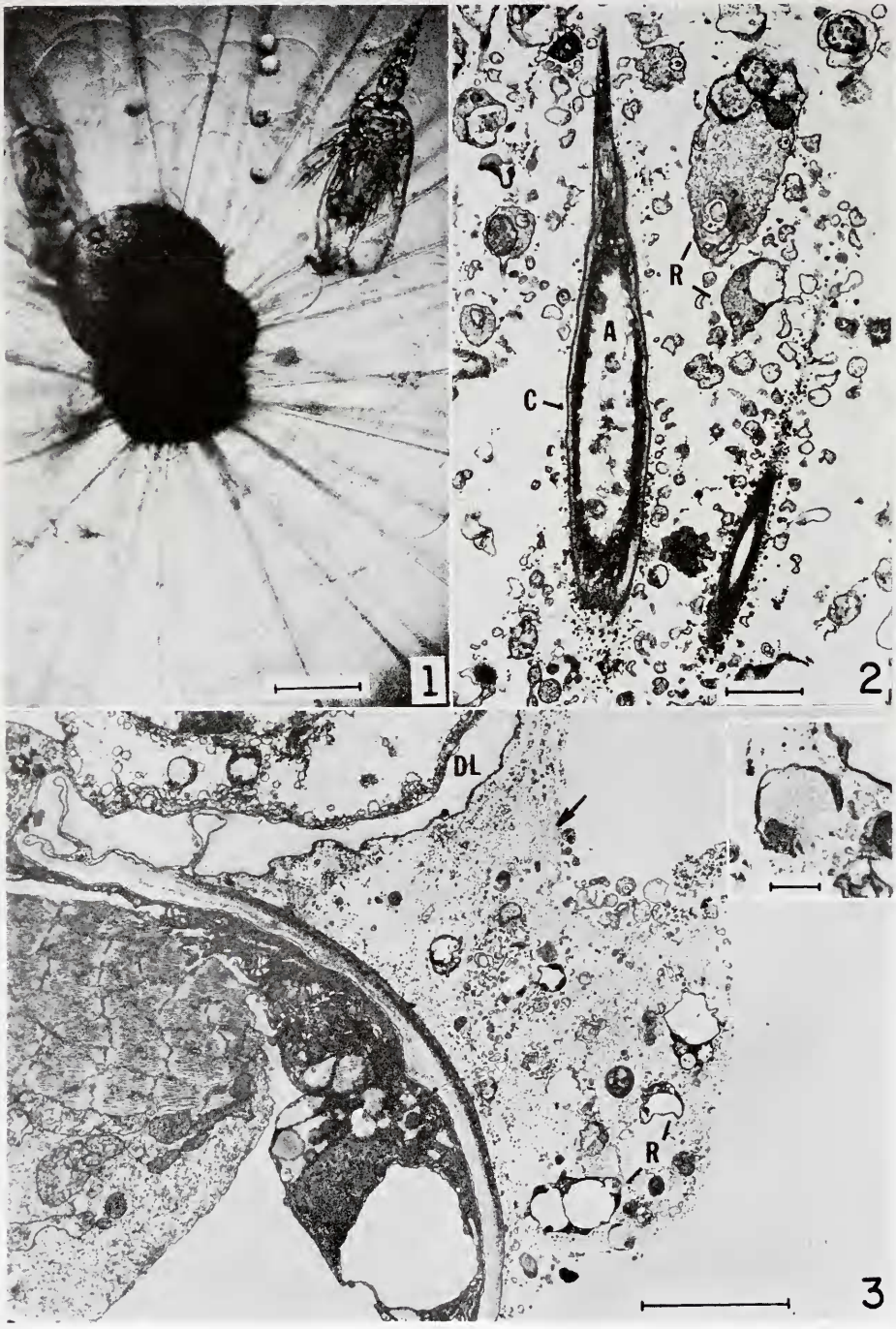
In spite of the significant role of planktonic foraminifera in marine food webs, little is known about their nutrition. Part of the lack of knowledge can be attributed to the difficulty in capturing uninjured specimens, which hampered previous attempts to culture them in the laboratory. By contrast, benthic foraminifera have been cultured for some time and their nutrition has been examined more thoroughly (*e.g.* Lengsfeld, 1969; Lee, 1974).

Recently, planktonic foraminifera have been successfully maintained in the laboratory for sufficiently long periods of time to enable observations of gametogenesis (Bé and Anderson, 1976) and nutritional studies. Although it is commonly assumed that planktonic foraminifera are predominantly herbivorous, it has been found that most of the spinose species are carnivorous and that only a few species are omnivorous. Omnivorous species sometimes capture diatoms and other small algae, but also prey on small crustacea which are snared within their weblike rhizopodia.

Rhumbler (1911) published colored drawings of planktonic foraminifera [*Hastigerina pelagica, H. digitata, Globigerina triloba* (= *Globigerinoides sacculifer*)] containing fusiform, pink, striated particles in their endoplasmic vacuoles. He identified these striated bodies as copepod muscle fibers. However, little attention seems to have been given to this pioneering observation. The present research has confirmed that these particles are pieces of muscle from prey.

Hastigerina pelagica was selected for the present study due to its abundance at the collection site, its robustness, and its ready acceptance of *Artemia* nauplii as food organisms in laboratory cultures. The nutritional habits of laboratory-cultured organisms and of specimens immediately obtained from the ocean are reported. The mode of capturing prey and the activity of rhizopodia in invading and engulfing prey tissue is examined. The cytochemistry of lysosomal activity in phagocytosis and digestion is presented.


1
A
C
R
2
DL
R
3

Materials and Methods

Collection and maintenance of specimens

Hastigerina pelagica was collected in glass jars by SCUBA diving near the surface approximately ten miles southeast of St. David's Battery, Bermuda, on July 9, 1975. Single specimens were maintained at the Bermuda Biological Station in pint-size jars containing millipore-filtered sea water. They were kept at 25° C under fluorescent illumination of a 12L:12D cycle. Three specimens of *H. pelagica,* which were fed *Artemia* (brine shrimp) nauplii cultured in the laboratory, were examined. One was fed eight hours and again two hours before fixation on July 28 to determine the early and late stages of prey capture and digestion. The remaining two were fed eight hours before fixation and were used for cytochemical studies of digestive enzyme secretion and distribution.

Preparation for electron microscopy

Specimens were fixed for 30 minutes at 3° C in 3% glutaraldehyde buffered with 0.2 M cacodylate buffer (pH 8.0). The cytochemical method of Gomori (1952) was used to detect lysosomal acid phosphatase. A NaF control was used to confirm the validity of the enzyme reaction product. Specimens prepared for transmission electron microscopy and cytochemistry were suspended in an agar matrix after glutaraldehyde fixation (and, where appropriate, after cytochemical preparation) to preserve the delicate rhizopodial strands. Specimens were post-fixed in 2% osmium tetroxide in 0.2 M cacodylate buffer (pH 8.0), stained with 2% uranyl acetate in 10% aqueous ethanol (except the cytochemical specimens), dehydrated in an ethanol series, cleared in propylene oxide and embedded in Epon. Ultra-thin sections were obtained with a Porter-Blum MT-2 ultramicrotome and collected on copper grids. Some of the sections were post-stained with Reynold's lead citrate. Sections were observed with a Philips EM-200 microscope operated at 60 kV.

Results

Light microscopic observations

Hastigerina pelagica is unique among the planktonic foraminifera in its possession of a bubble capsule, resembling a mass of soap bubbles, that completely surrounds its shell (Fig. 1). An adult *H. pelagica* has a shell length of about

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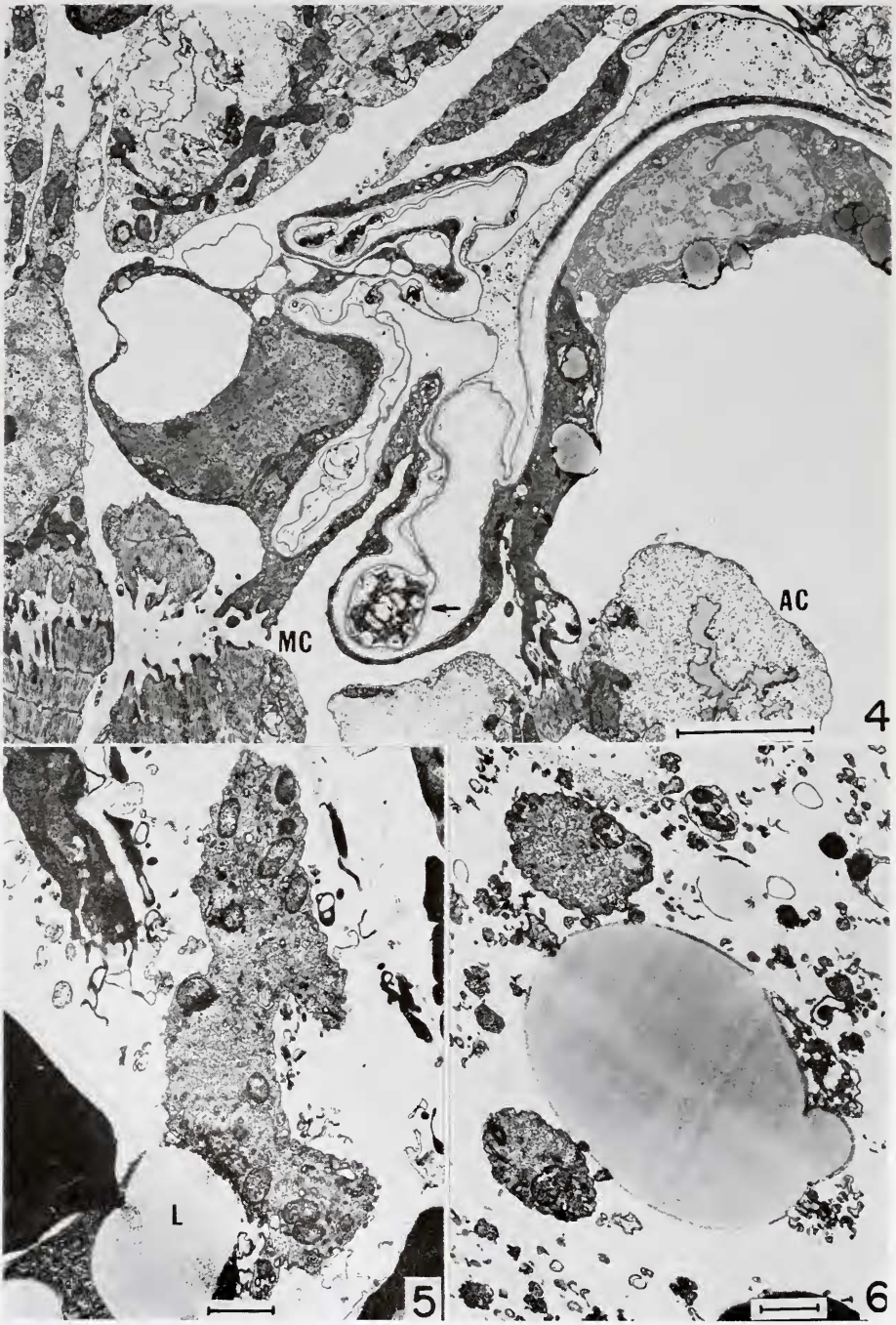
FIGURE 1. A snared copepod has been drawn into the bubble capsule of *Hastigerina pelagica* shortly after being collected. Closely packed bubbles surround the shell (lower left) and its radially arranged spines. Scale bar equals 0.25 mm.

FIGURE 2. An electron micrograph of a section through the appendages (A) of a snared *Artemia* nauplius shows the abundance of rhizopodia (R) near the surface (c) of the prey; scale bar equals 1 μm.

FIGURE 3. The surface of a captured *Artemia* nauplius is covered with adhesive substance (arrow) secreted on the double-layered cuticle (DL) by rhizopodia (R). Insert at upper right shows the release of adhesive substance from a vacuole within a rhizopodium. Scale bar equals 4 μm; inset scale bar equals 0.5 μm.


MC
AC
4
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6

1 mm and a spine length of about 12 mm. Hence, the total diameter of a floating specimen is about 25 mm. The capsule in adult specimens has an average diameter between 2 and 3 mm and consists of numerous bubble compartments that are stacked on top of each other. In general, the bubbles are spherical and approximately 200 μm in diameter, but they may be flattened along contact surfaces between bubbles.

A large proportion of captured *H. pelagica* specimens have one or more copepods lodged inside their bubble capsules (Fig. 1). Frequently the copepods are completely digested, as only empty carapaces remain visible. *H. pelagica's* carnivorous habit is readily demonstrated by the introduction with a pipet of copepods (*e.g., Oncaea* sp. and *Farranula* sp.) to floating specimens in culture. Healthy, freshly-collected *H. pelagica* will capture copepods when the latter come into contact with its network of rhizopodia, which extend through the capsule and occur along, as well as between, the spines.

H. pelagica and other planktonic foraminifera also feed on *Artemia* (brine shrimp) nauplii in the laboratory. When an *Artemia* touches a spine, it immediately adheres to the sticky rhizopodia and is frequently rendered helpless within seconds. Few specimens escape once they have been snared. Within a short duration, usually about 30 minutes, the crustacean is transported by the rhizopodia along the spine to the bubble capsule. As the prey is carried into the capsule, the bubbles are displaced. The crustacean can be held anywhere in the bubble capsule and is not oriented in any particular way relative to the shell aperture. The crustacean is mechanically disrupted by the rhizopodia which invade the soft tissue and begin digestion outside of the test. Some of the dislodged tissue is carried into the test where further digestion occurs.

Copepod carapaces are ejected from the bubble capsule several hours after capture and following complete digestion. This is not the case for *Artemia,* whose nauplii possess a very thin cuticle (Hootman, Harris and Conte, 1972) ; portions of the cuticle are ejected continuously as invasion and digestion of prey tissue occurs.

Electron microscopic observations

Rhizopodial attachment to prey outside the bubble capsule. The first stage of capture involves rhizopodial attachment to the prey (Figs. 2–4). Fine strands of rhizopodia (R in Figs. 2 and 3) are congregated in the vicinity of the small appendages (A) of the prey. Many of these strands are so fine that they cannot be resolved with the light microscope, but are clearly visible with the electron microscope. The cuticle (C) of the *Artemia* nauplius appendage exhibits a thin electron dense outer layer (*ca.* 29 μm thick) and a thicker irregular layer beneath it about 0.2 μm thick. Considerable variation occurs in morphology and diameter

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FIGURE 4. Rhizopodia (arrow) congregate within the inner-most recesses of the *Artemia* cuticle and eventually penetrate into the underlying adipose tissue (AC) and muscle tissue (MC). Scale bar equals 5 μm.

FIGURE 5. A rhizopodium containing characteristic tubular mitochondria attaches to an extruded lipid droplet (L). Scale bar equals 1 μm.

FIGURE 6. An extruded lipid body is surrounded by rhizopodia which have transported it away from a lysed cell; scale bar equals 1 μm.

of the rhizopodia. The larger strands, approximately 102 μm diameter, contain a granular cytoplasm with small tubular mitochondria (*ca.* 0.5 μm diameter). Occasional microtubules, and endoplasmic reticulum are also observed. Mitochondria in the cytoplasm within the shell are about 1 μm in diameter and therefore are somewhat larger than those seen in small rhizopodia. Very fine rhizopodia (*ca.* 0.05–0.2 μm) contain no discernible organelles. The small rhizopodia occur abundantly near the surface of the prey. These are probably very small branches from the larger rhizopodia.

Rhizopodia in the vicinity of broad surfaces on the *Artemia's* body secrete a fibrous mass of adhesive substance which adheres to the prey (Fig. 3). This material undoubtedly strengthens the attachment of the rhizopodia to the surface of the prey and reinforces the rhizopodial strands by providing a matrix between them. Evidence for secretion of the adhesive substance by rhizopodia is presented in the enlarged inset in Figure 3. A vacuole containing a fine fibrillar mass of adhesive substance has ruptured releasing its content. Rhizopodia of various diameters occur within the adhesive matrix and some of them contain mitochondria and large empty vacuoles.

The cuticle surrounding the body region in *Artemia* nauplii consists of a double layer (DL) of thin electron dense lamellae with a fairly electron translucent space between them. The surface of the cuticle is rugose and forms deep crevices and fissures. Immediately beneath the exoskeleton is a layer of epithelial tissue connected to muscle cells or adipose tissue. Very fine rhizopodia (arrow in Fig. 4) and the adhesive substance penetrate deep into the crevices of the cuticle (Figs. 3 and 4). Muscle fiber cells (MC) and adipose cells (AC) containing lipid are also visible within the body cavity. The remarkable tenacity with which the foraminifera holds its prey can be attributed to the massiveness of the rhizopodial attachment, their deep penetration into crevices of the prey and their reinforcement through secretion of the adhesive substance.

Rhizopodial invasion of prey tissue. The extension of rhizopodia into *Artemia's* cuticle crevices eventually leads to penetration within the body cavity. Within eight hours after capture of prey, electron microscopic examination shows penetration of rhizopodia inside the cuticle and surrounding epithelial cells containing lipid reserves (in Figs. 5 and 6). The rhizopodia are readily distinguished from prey tissue by their irregular margin and tubular mitochondria which are typically protozoan. Many of the cells within the body cavity where rhizopodia have invaded appear moribund, because they possess an electron dense granular cytoplasm, contain few intact organelles and some of their lipid droplets appear to be extruded through the lysed cell membrane.

Ingestion of tissue fragments by rhizopodia. Rhizopodial invasion of the prey is followed by engulfment of prey tissue within food vacuoles. Lipid droplets released from *Artemia* cells within the body of the prey are surrounded by rhizopodia (Fig. 6). Some produce prong-like projections that invade the surface of the lipid droplet. Adhesive substance is also released within the body cavity of the prey. The lipid droplets, masses of *Artemia* cells and shattered segments of cuticle are transported by the rhizopodia away from the body of the prey. The digestible substances such as lipid and cell material are sequestered within rhizopodial vacuoles and carried within the aperture of the foraminifer. Large sheets of cuticle (arrows in Fig. 7) dislodged from the prey are shown

being transported away by the rhizopodia and are apparently discarded at the periphery of the ectoplasm. Food vacuoles containing cellular material from the prey are carried into the earliest chambers of the foraminiferal shell, indicating that ingestion and digestion occur throughout the intrashell cytoplasm. A small chamber (Fig. 8) which is one of the oldest and farthest removed from the aperture contains a large food vacuole (FV) approximately 20 μm diameter and smaller ones nearby that are 4.7 μm diameter. The shell (S) has been decalcified during preparation for electron microscopy, but the organic lamellae within the wall remain.

Formation of digestive vacuoles. The food vacuoles within the endoplasm are converted to digestive vacuoles as indicated by lysis of sequestered food particles and the presence of lysosomal enzymes marked by acid phosphatase reaction product (X) (Fig. 9). The larger digestive vacuoles are 4.5–6.0 μm in diameter, which agrees with the diameter of food vacuoles observed in Figure 8. The small vacuoles containing reaction product are primary lysosomes and have a typical diameter of 0.5–0.7 μm.

In addition to digestive vacuoles contained in the endoplasm, conversion of food vacuoles into digestive vacuoles while they are still in the rhizopodial network can sometimes be seen.

Origin and role of adhesive substance. The adhesive substance used to capture prey originates in the Golgi apparatus within the endoplasm. In conventional, stained electron microscopic preparations of *H. pelagica,* the Golgi contains fine fibrous deposits in the cisternae and distended saccules on its maturing face (the surface containing enlarged vacuolar spaces which appears as the concave surface in Fig. 10). The fibrous deposits are also present in vacuoles (V) near the Golgi in Figure 10. These adhesive-containing vacuoles are apparently transported outward into the rhizopodia to aid in capture of prey. The Golgi, therefore, serves remarkably diverse secretory roles. It secretes lysosomal enzymes as part of the digestive apparatus and can also produce adhesive substance (possibly mucoid).

Lysosomal distribution. Lysosomes (Ly) secreted in the endoplasm within the shell are carried into the rhizopodia outside of the shell (Fig. 11) and in the thin cytoplasmic partitions forming the bubble capsule. The large number of lysosomes in the rhizopodia and the presence of occasional masses of cytochemical reaction product (X) in the lacunae between the rhizopodial strands (Fig. 12) suggest that extracellular enzymes may be secreted to kill and help dislodge cells from the prey. Masses of prey tissue (CM) are present in the lacunae and are already in contact with lysosomal enzymes. It is not possible to determine how the enzymes (marked by reaction product) were released into the lacunae. They may have been secreted there directly by primary lysosomes or they could be excess enzymes released during defecation of residual digestive vacuoles.

Association with microamoebae. During the course of the cytochemical investigation, a small amoeboid cell was noticed (*ca.* 5 μm in diameter) among the foraminiferal rhizopodia (A in Fig. 11). This is clearly not a part of the rhizopodial network, since it possesses its own nucleus and presents a typical amoeboid cytoplasmic fine structure. One of its large vacuoles contains reaction product (X) and amorphous material that appears to be in a late stage of digestion. Additional reaction product appears in small vesicles on the opposite side of the cell and these look like primary lysosomes. This may be a free-living amoeba that

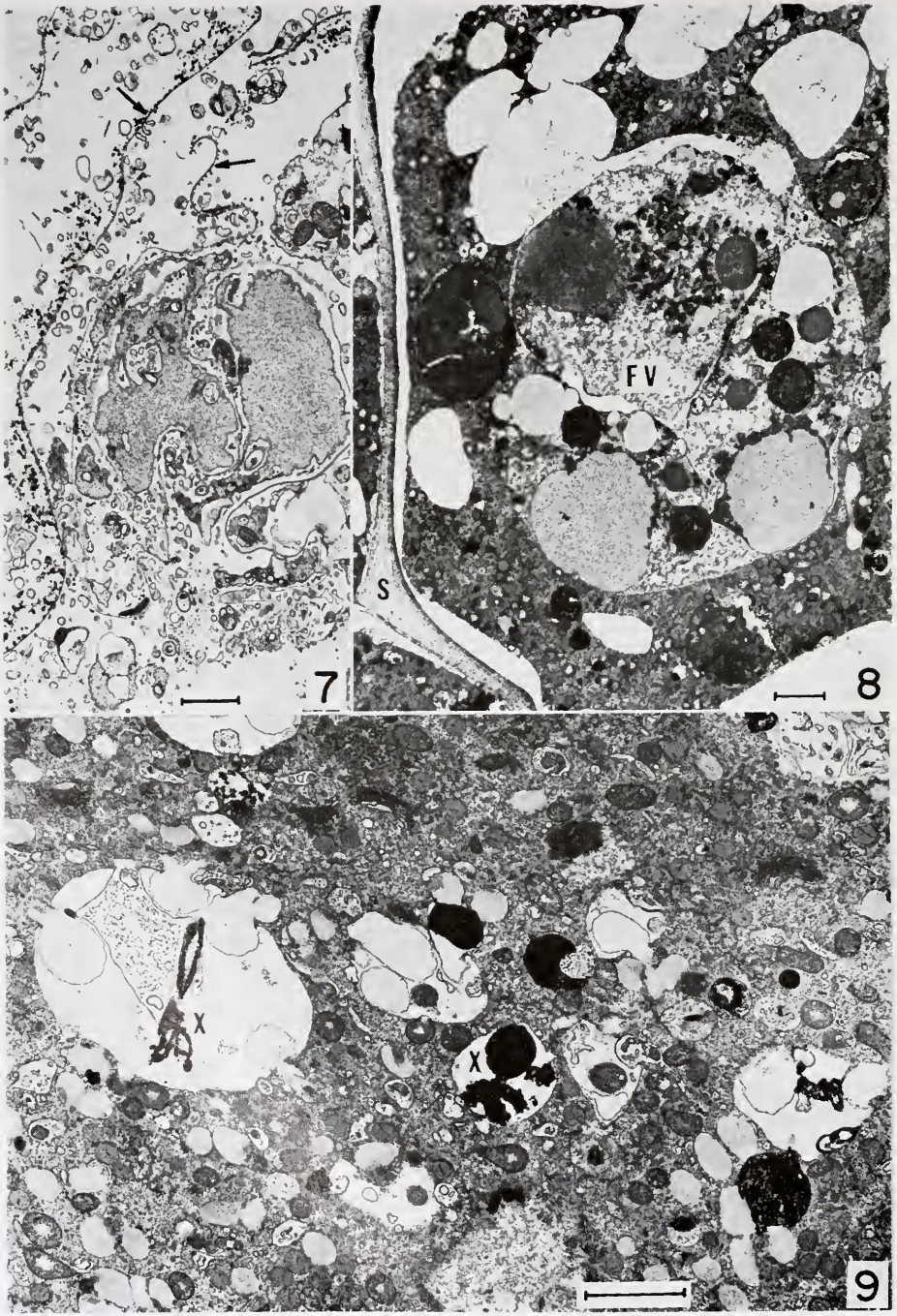

FIGURE 7. Rhizopodia surround sheets of cuticle (arrows) that have been torn from the prey and are being carried away to be eventually discarded. Scale bar equals 1 μm.

has established a commensal association with the foraminifer. There is no evidence that these small amoebae are parasites. Moreover, samples have been taken of foraminiferal rhizopodial cytoplasm with surrounding culture fluid and inoculated into sterile F/8 medium (Guillard and Ryther, 1962). The inoculum produced an algal bloom and numerous small amoebae which appeared to feed on the algae. It is concluded that the amoebae in the rhizopodial network are capable of an independent existence but have assumed a scavenger role in the foraminiferal ectoplasm, engulfing small particles of food not taken by the foraminifer. The presence of these microamoebae within the ectoplasm of *H. pelagica* may indicate an interesting ecological adaptation between two environmentally compatible Sarcodina.

Discussion

The ingestion of food particles by enclosing them in cytoplasmic vacuoles (phagocytosis) is a well-established nutritional mode among the Sarcodina (Jepps, 1956; Hall, 1965; Grell, 1973). However, little is known about the mechanisms of food capture and ingestion in floating species that produce rhizopodial networks. The rhizopodia-bearing species are clearly different from lobopodia-bearing species such as amoebae, which surround their prey or pinch it into small fragments before ingestion. *H. pelagica* illustrates the facile mechanism of rhizopodia-bearing species in snaring prey, dislodging manageable segments of tissue and engulfing food particles in food vacuoles in the rhizopodial network. This network extends far beyond the perimeter of the organism's shell and forms a three-dimensional, sticky web that efficiently tangles prey coming within its bounds. The rapid cessation of struggle by the prey suggests that the foraminifer secretes a narcotizing agent, but there is no direct evidence of it at present.

The presence of an adhesive substance may serve several roles other than reinforcement of attachment. The adhesive material occurs in Golgi secreted vacuoles and sometimes is observed in close proximity to lysosomes. The fine fibrous secretion emitted in the prey tissue may help to contain extra-cellular enzymes at the site of attack and thus increase their efficiency and conserve their concentration. Moreover, it is known that many digestive enzymes are acid hydrolases which have a pH optimum near 5. Sea water is alkaline and is not a suitable environment for acid hydrolase activity unless some mechanism is established to create microenvironments with acid pH. If the adhesive material contains acid mucopolysaccharides, they may create acidic microenvironments surrounding the fibrous substance that enhances digestive enzyme activity. Extracellular acid phosphatase reaction product has been observed in regions of rhizopodial attack on prey and in lacunae among the rhizopodia outside of the shell.

Figure 8. A food vacuole (FV) occurs in the innermost portion of cytoplasm within a small chamber of the foraminiferal shell (S). Scale bar equals 2.5 μm.

Figure 9. Digestive vacuoles containing digestive enzymes (indicated by cytochemical reaction product, X) contain remains of digested prey. The digestive vacuoles are formed from food vacuoles by fusion with lysosomes containing the digestive enzymes; scale bar equals 1 μm.

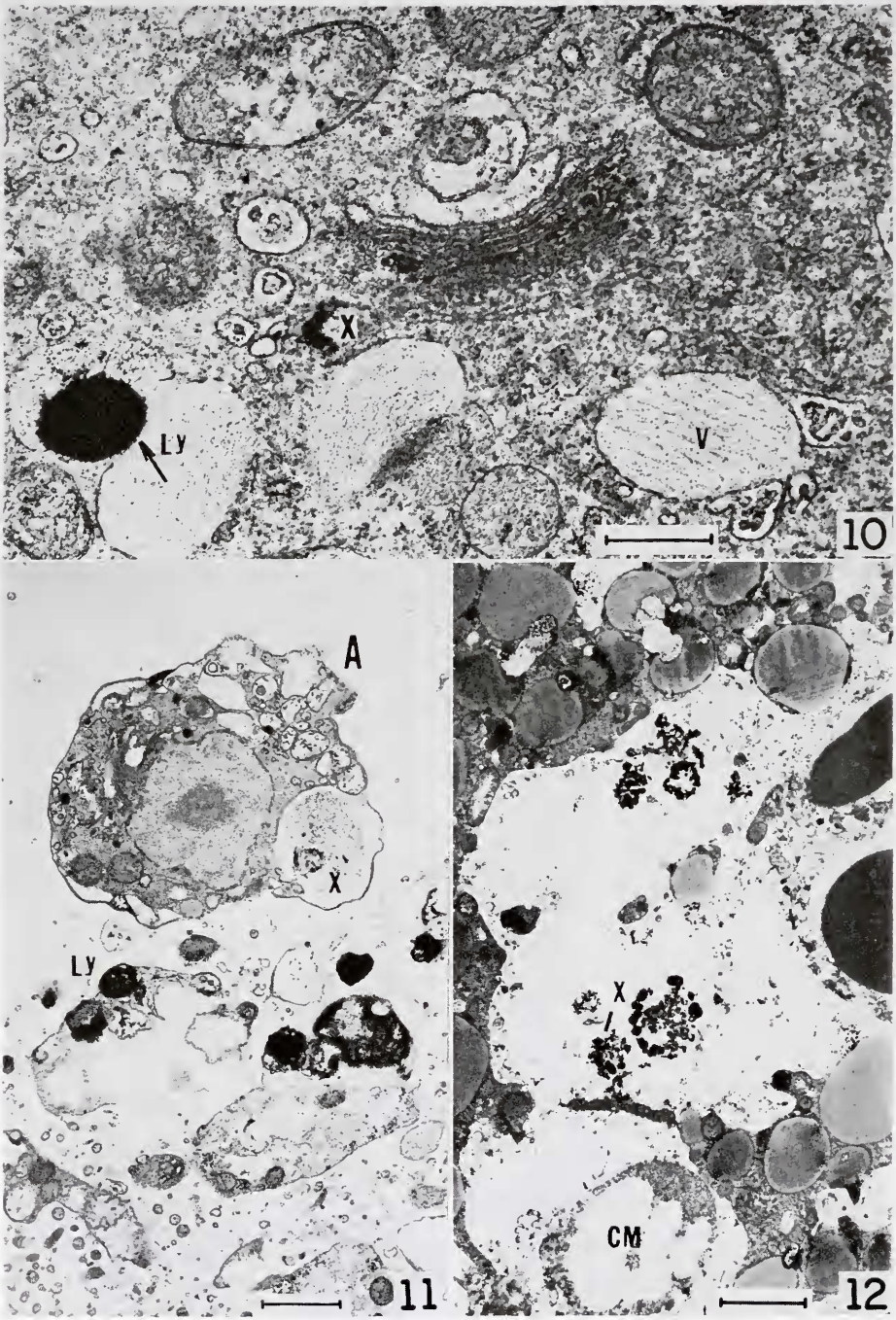

FIGURE 10. Lysosomes originate in the Golgi apparatus as shown by the presence of cytochemical reaction product (X) within the peripheral saccules of the Golgi and in nearby

Some digestion of the prey can occur in the lacunae in addition to digestion within digestive vacuoles in the endoplasm. Foraminifera purge their cytoplasm of undigested waste material by carrying it out of the aperture in residual vacuoles which stream along the rhizopodia and are released at some distance from the shell (Anderson and Bé, 1976). It is possible that defecation near the aperture will also contribute residual digestive enzymes to be used in preliminary digestion of newly ingested food within rhizopodial lacunae. If such reuse of digestive enzymes does occur, it demonstrates a remarkable cellular economy.

Lengsfeld (1969) has suggested that digestion in the benthic foraminifera *Allogromia laticollaris* occurs solely in the branching rhizopodial lacunae rather than in digestive vacuoles. However, her observations are based on noncytochemical preparations, and therefore it is difficult to assess the validity of her hypothesis. In *H. pelagica,* there is evidence that the digestive vacuoles are completely membrane-bound, since sequential sections taken through a digestive vacuole region show little evidence of canal-like connections among the vacuoles. Moreover, cytochemical evidence for digestion in these vacuoles is presented in this study.

It is not possible to determine what proportion of the digestive vacuole activity is due to hydrolases secreted by the foraminifer as opposed to endogenous lysosomal enzymes of prey cells released during cell death. Thus, part of the digestion may be due to autolysis and part to predator hydrolases secreted into the digestive vacuoles. The presence of Golgi-secreted lysosomes in phagotrophic protozoa has been well established by electron microscopic cytochemical studies (Goldfischer, Carasso, and Favard, 1963; Elliot and Clemmons, 1966; Stoltze, Lui, Anderson and Roels, 1969).

There is a remarkably selective activity of the rhizopodia during capture and engulfment of prey. Some rhizopodia sever large masses of cuticle from the prey which are torn away and carried some distance. However, little of this nondigestible material is transported into the intrashell cytoplasm, as occurs with the digestible soft tissue. When small prey (several μm in size) containing a shell are captured, they may be carried whole into the foraminiferal cytoplasm where they appear within a digestive vacuole. The basis for this selective behavior by the rhizopodia is not known but certainly constitutes one of the most remarkable and potentially illuminating adaptations exhibited by these unicellular organisms. There is no fine structure characteristic that separates food-carrying rhizopodia from those dislodging sheets of cuticle. It must be presumed that the differential response is determined by chemotactile stimulation. The nature of membrane chemoreceptors, if present, has not been investigated to the best of our knowledge. The intensity of rhizopodial activity in feeding also appears to be modulated according to the nutritional state of the foraminifer. When it is well-nourished, invasion of prey tissue and its ingestion may last for many hours. The

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secretory vesicles (Ly). Adhesive substance also occurs abundantly in vacuoles (V) in the Golgi region; scale bar equals 0.5 μm.

FIGURE 11. A microamoeba (A) containing a digestive vacuole (X) was observed living amidst the foraminiferal rhizopodia containing lysosomes (Ly); scale bar equals 1 μm.

FIGURE 12. Digestive enzymes marked by reaction product (X) are released into lacunae with the rhizopodial network surrounding masses of cellular material (CM) dislodged from the prey; scale bar equals 2 μm.

specimens used in this study were well nourished and some digestion of prey was observed as much as eight hours after snaring it. In poorly nourished specimens, invasion and digestion of prey can occur within a few hours after it is snared.

The web-like shroud of rhizopodia in *H. pelagica* and their remarkably facile ability to snare prey and separate food particles from nondigestible substances represents an elegant adaptation to a floating marine existence. The wide range of food accepted and the ability of the foraminifers to snare and subdue motile prey of nearly half their size bear witness to their robustness and adaptability to diverse nutritional demands.

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Summary

The fate of *Artemia* (brine shrimp) nauplii offered as food to *Hastigerina pelagica* in laboratory cultures was determined using light and electron microscopy.

Contact between prey and foraminiferal rhizopodia leads to immediate attachment. Adhesive substance is secreted and rhizopodia invade crevices of the prey. penetrate beneath the cuticle, and begin disruption of prey tissue. Some tissue masses and cells are dislodged and digestion is begun outside of the test as indicated by lysosomal enzymes surrounding partially degraded prey tissue within spaces created by surrounding rhizopodia. Dislodged prey tissue is sequestered into food vacuoles and carried into the intrashell cytoplasm where digestion also occurs. The digestive enzymes are secreted by the Golgi apparatus in membrane-bound vesicles (lysosomes) which are carried throughout the cytoplasm and fuse with the food vacuoles to produce digestion. The carapace or cuticle of digested prey is discarded and undigested waste material in residual vacuoles is defecated at the periphery of the rhizopodial network.

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